Prevalence of potential vectors of yellow fever in the vicinity of Enugu, Nigeria

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RÉSUMÉ

IMPORTANCE DES VECTEURS POTENTIELS DE FIÈVRE JAUNE DANS LE VOISINAGE D'ENUGU AU NIGÉRIA

A Enugu et dans ses environs les auteurs ont étudié durant treize mois consécutifs et dans quatre biotopes différents : urbain, forestier et ruraux, la répartition et l'importance des Stegomyia *vecteurs connus ou soupçonnés de fièvre jaune.*

*La prévalence des adultes a été estimée par des captures sur appât humain et l'oviposition par des pondoirs-pièges faits de récipients en verre noir (modèle CDC) et de bambous coupés. Les pondoirs-pièges en verre ont prouvé leur efficacité pour établir la prévalence d'*Aedes aegypti *dans des biotopes variés, habités ou non; mais ils sont beaucoup moins attractifs vis-à-vis des espèces sauvages, de même que les bambous. Au cours de la dernière saison des pluies, les auteurs ont constaté que le rendement des pondoirs-pièges dépendait du nombre de mises en eau, le chiffre standard de trois étant sous-estimé de 50 % pour les espèces sauvages et* A. simpsoni *demandant au moins 9 mises en eau pour l'éclosion complète des œufs.*

*Des 13 espèces d'*Aedes *capturées sur appât humain dans les villages ruraux en région boisée,* A. africanus, A. luteocephalus *et* A. aegypti *sont les plus abondants, suivis de* A. simpsoni. *En ville,* A. aegypti *représente plus de 80 % du total des captures d'adultes. En zone rurale et forestière* A. africanus *représente 60 à 80 % des captures sur appât humain.*

*Au niveau du sol, l'activité d'*A. africanus *et* luteocephalus *est surtout restreinte aux heures crépusculaires alors que celle d'*A. aegypti *est davantage diurne et augmente graduellement à l'approche du lever du soleil. Dans les 2 villages ruraux le taux crépusculaire de piqures de ces trois vecteurs ensemble atteint plus de 2 par heure et par homme, pour une période de 10 mois, de mars à décembre.*

MOTS-CLÉS : *Aedes* - Capture - Piégeage - Adultes - Œufs - Larves - Cycle d'activité - Nigéria.

ABSTRACT

Studies were performed over 13 consecutive months in four different biotopes, one urban, one forest and two rural, in the Udi Hills and nearby Enugu, to determine the distribution and prevalence of known and suspected Stegomyia *vectors of yellow fever. The prevalence of adults was assessed by human-bait collections, and their ovipositing activity by bamboo cups and CDC black-jar oviposition traps. The ovitraps proved to be highly effective in monitoring the prevalence of* Aedes aegypti *in various biotopes, whether inhabited or not, but were less favoured by the feral species, a characteristic shared by bamboo cups. The yield of ovitraps exposed in the late rainy season depended on many repeated soakings of the paddles, the standard 3 soakings underestimating the feral species by one-half, and* Aedes simpsoni *requiring at least 9 soakings for a complete hatch of eggs.*

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Among 13 Aedes *species caught from human baits in wooded rural villages,* Ae. africanus, Ae. luteocephalus *and* Ae. aegypti *were the most abundant, followed by* Ae. simpsoni. *In the urban biotope,* Ae. aegypti *comprised over 80 % of the total adult captures. In the rural and forest biotopes,* Ae. africanus *comprised 60-80 % of the captures on human bait. At ground level the biting activity in outdoor populations of* Ae. africanus *and* Ae. luteocephalus *was mainly restricted to the crepuscular hours, while that of* Ae. aegypti *was more diurnal and increased gradually towards sunset. In the two rural villages, the crepuscular biting rate of these three known vectors combined was more than two females per man-hour for a period of 10 months from March to December.*

KEY WORDS : *Aedes* - Catching - Trapping - Adults - Eggs - Larvae - Activity cycle - Nigeria.

INTRODUCTION

In tropical Africa, yellow fever is transmitted not only by *Aedes aegypti* but also by other species of the subgenus *Stegomyia*, which are particularly important in rural epidemics. Notable examples are the Ethiopian epidemic of 1960-1962 in which *Ae. africanus* and *Ae. simpsoni* were the vectors, the Sudan epidemic of 1940 transmitted by *Ae. vittatus*, and the Nigeria epidemic of 1969 on the Jos plateau in which *Ae. luteocephalus* was implicated (Lee & Moore, 1972). In Nigeria, although ecological studies have been made on the *Stegomyia* mosquitos of southwestern Nigeria (Mattingly, 1949; Boorman, 1960), of northwestern Nigeria (Service, 1963, 1974) and the Jos plateau (Boorman, 1961; Lee *et al.*, 1974), no such studies had hitherto been made in southeastern Nigeria, where an extensive outbreak of yellow fever took place in 1951-1952 in a rural area to the west of Enugu Ngwo (MacNamara, 1954).

Therefore, the WHO Arbovirus Vector Research Unit gave high priority in its research programme to ecological studies of the distribution and prevalence of potential vectors in different biotopes so that the entomological conditions calling for vector control can be recognized and determined when and where they occur. It was thus essential to standardize sampling techniques, so that they can be employed to collect valid base-line information and subsequently to evaluate control measures applied in different environments. These studies were conducted for an uninterrupted period of 13 months from November 1974 to November 1975 inclusive in four different biotopes near Enugu, Nigeria.

METHODS

Study Sites : The four sites consisted of one located in an urban area of Enugu town (Ogui) and three sites located in the Udi Hills (6° 29' N, 7° 23' E) some 20 km north of Enugu, namely two rural communities (Egede and Abor) and one forest relict. This forest relict, less than 2 km in extent, is separated from Abor village by a highway, and the entire area is surrounded by savanna grassland. The relict is characterized by relatively undisturbed secondary forest with a fairly continuous canopy at a height of 15-20 m. The understory is dense with numerous species of plants including shrubs and climbers. Unlike the neighbouring villages, these communities lack palm trees and banana plants.

Human-bait Catches : The biting and landing densities of adult female mosquitos were determined by monthly crepuscular and 24-hour catches. The crepuscular catches were made outdoors, usually under trees, by three teams of two scouts per team. This schedule was followed in all four areas on two consecutive evenings for four hours, starting two hours before sunset. In the Enugu district, sunset time ranges between 18 h 10 in November and 18 h 50 in July. In each area, three catching stations were established at least 300 m apart. The 24-hour collections were performed at two sites (Abor village and Abor forest relict) by two 4-man teams rotating at 4-hour intervals, starting nine hours before sunset and continuing for 25 hours. The catches made during the first hours were discarded to avoid the "intrusion effect" when team scouts take their places at the catching station (Germain, *et al.*, 1973). In both types of collection the captures were recorded hour by hour.

Larval Surveys in Bamboo Cups : At each of the 4 sites, a set of 20 bamboo cups, weathered for 4-5 weeks and sterilized, were nailed to trees at least 25 m apart at 1.5 m height in each of the four study sites. Every week all the larvae present in the cups were collected, and the cups were filled with fresh water. More water was added five days later, and thus the original water level was restored twice per week. The numbers of larvae identified were recorded for each cup, so that the percentage of cups positive for different species was determined along with the number of larvae of each species.

CDC Ovitraps : At each of the 4 sites, 20 CDC ovitraps (Fay & Eliason, 1966) were placed in empty cans and secured in position by nailing the cans to the tree trunks at 1.5 m height alongside the bamboo cups. In the urban and the two rural sites, further sets of 20 ovitraps were placed under house roofs or eaves in 10 selected compounds. In the forest relict site, 20 traps were set at ground level near the trees where the bamboo cups were hung. New paddles were inserted in the ovitraps every week, and collected after an exposure of two days. Each paddle was individually wrapped with clean paper, placed in a vinyl bag, and kept in the laboratory for three days before being examined for the presence of eggs. In order to obtain a hatch of larvae, the paddles were immersed for 2 days in tap water (which had been sedimented for 4-6 days). They were then removed, leaving the hatched larvae in the water, and allowed to dry for 5 days before being again immersed for 2 days. In all the ovitrap collections of the 13-month study, paddles were treated with 3 soaking immersions at weekly intervals, and thus the prevalence figures reported are based on that treatment. However, a special investigation where they were treated with 9 weekly immersions is described below under Results, along with an evaluation of what the effect of this prolonged treatment would have been on the prevalence figures.

TABLE I

Numbers of the various mosquito species caught in the total of 13 monthly crepuscular collections on human baits, expressed as No. per 100 man evenings.

	Study sites			
	Ogui	Egede	Abor	Forest relict
Ae. aegypti	274.4	82.1	111.5	50.0
Ae. africanus	0	521.2	912.3	109.2
Ae. luteocephalus	61.5	78.2	239.2	12.3
Ae. simpsoni	5.8	1.3	0.8	0.8
Ae. vittatus	0.6	0	0	0
Ae. dendrophilus	0	0	0.8	0
Ae. abnormalis	0.6	3.2	0.8	3.1
Ae. domesticus	0	0.6	0.8	0.8
Ae. tarsalis	0	1.3	1.5	1.5
Ae. fowleri	0	1.9	0.8	1.5
Ae. stokesi	0	0	0	0.8
Ae. furcifer/taylori	0.6	2.6	0	0
Ae. circumluteolus	0	1.3	6.9	1.5
Ae. palpalis	0	0.6	0.8	0.8
Ae. ingrami	0	0.6	0	3.8
Ma. africana	0	1.3	13.1	13.1
Culex spp.	34.0	125.6	50.8	253.1
E. chrysogaster	0.6	3.2	1.5	0.8
Total for first five *Aedes (Stegomyia)* spp.	342.3	682.8	1 263.8	172.3

RESULTS

Adult Density : In the crepuscular collections (Table I) 16 mosquito species were caught in the two rural communities as compared to 8 in the Ogui urban area. Moreover, a greater variety of *Aedes (Stegomyia)* species were collected in the wooded than the urban sites. Of the 15 *Aedes* species identified, *Ae. aegypti, Ae. luteocephalus* and *Ae. africanus* were the most abundant in both the crepuscular and the 24-hour collections. In sylvatic environments, whether inhabited or not, the highest proportion was *Ae. africanus* (60-80 %) which exceeded that of the other two known vectors. This species was completely absent in Ogui, where 80 % of the total catch was *Ae. aegypti* (Table 2). The number of *Ae. luteocephalus* caught in the rural communities equalled or exceeded that of *Ae. aegypti*. In Abor village, the proportion of *Ae. luteocephalus* caught in the crepuscular collections (19 % of the total *Stegomyia* catch) was about twice that of *Ae. aegypti* (9 %), although only one-quarter as great as the captures of *Ae. africanus* (72 %). In the forest relict, *Ae. luteocephalus* accounted for 7 % of the *Stegomyia* in the crepuscular catches, but only 1.4 % in the 24-hour catches. The known vector *Ae. simpsoni* was taken in these human-bait collections only in small numbers, the highest prevalence being in urban Ogui where it constituted 6 % of the total captures. *Ae. apicoargenteus* and *Ae. dendrophilus*, taken in quantity in ovitraps and bamboo cups, were almost completely absent from the human-bait catches (Table I and II).

Biting Cycles : For the 24-hour collections (Fig. 1), the geometric mean (Mw) for the catches in each hour was calculated from the 13 monthly figures and then converted to the number per 100 man-hours for plotting on a logarithmic scale. Two wooded localities, Abor and the forest relict were thus compared for the 24-hour cycle of the three most prevalent arbovirus vectors.

Aedes aegypti in Abor became increasingly active in the afternoon, the activity reaching a peak three hours before sundown, and continuing for 2 hours after dark; it showed a minor peak at sunrise and early morning, which amounted to 5 % of the total captures as compared to 83 % in the afternoon peak. By contrast, in the forest relict the activity peaked in the last hour of daylight and ceased completely before sundown, while there was no activity in the early morning.

Ae. africanus in both localities began to arrive on human baits three or four hours before sunset and continued landing for two hours after sunset (Fig. 1); however, nearly 60 % of the total activity occurred during the two hourly periods immediately before and after sunset. The number caught in the hourly period immediately after sunset was greater than that immediately preceding sunset, the difference being 3-fold in the forest relict but only 20 % at Abor village. Although there were some catches during the morning hours, the numbers were less than 5 % of the total females caught.

Ae. luteocephalus at Abor confined its activity almost completely to the twilight hours, resembling the prece-

TABLE II

Frequency distribution of the six most common *Stegomyia* species taken in four different biotopes by different sampling methods : percent of the total collected.

Locality	Collecting methods (1)	No. *Aedes* species collected	*aegypti*	*luteo-cephalus*	*africanus*	*simpsoni*	*apicoar-genteus*	*dendro-philus*
Ogui (Urban)	Crepuscular	6	80.1	18.0	0	1.7	0	0
	b/t	4	52.1	43.9	0	3.7	0	0
	c/t	5	81.1	17.7	0	0.9	0.1	0
	c/c	3	94.7	5.0	0	0.3	0	0
Egede (rural)	Crepuscular	14	12.0	11.5	76.3	0.2	0	0
	b/t	10	12.9	5.9	0.8	6.1	74.1	0.1
	c/t	4	10.4	1.3	0	1.8	86.4	0
	c/c	4	94.2	2.5	0	1.1	2.2	0
Abor (rural)	Crepuscular	12	8.8	18.9	72.1	0.1	0	0.1
	b/t	10	19.0	4.1	0.1	3.6	71.3	2.0
	c/t	6	18.2	1.2	0	6.7	73.9	0
	c/c	5	87.8	4.3	0	0.3	7.5	0
Forest relict	Crepuscular	14	29.0	7.1	63.4	0.4	0	0
	b/t	12	10.1	1.4	2.9	0.4	53.3	31.8
	c/t	7	8.9	0.7	0.1	0.2	89.2	0.9
	c/g	7	33.0	6.4	5.6	0.8	49.0	5.1

(1) b/t : bamboo cups in trees; c/t : CDC ovitraps attached to trees at 1.5 m height; c/c : CDC ovitraps in compounds; c/g : CDC ovitraps placed on ground.

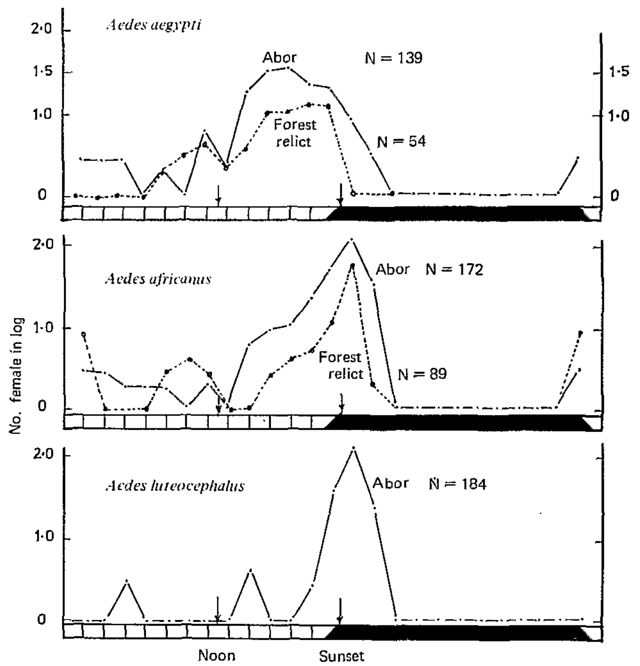

FIG. 1. — Average hourly captures of the three most common *Stegomyia* species landing on human baits in two different biotopes near Enugu : taken from a total of 13 monthly collections.

ding species in showing its peak (45 %) in the hourly period immediately following sunset. Over 92 % of the total catch was taken during the four crepuscular hours, as compared to 80 % for *Ae. africanus* and 38 % for *Ae. aegypti.*

Larval Prevalence in Bamboo Cups : The abundance of 6 *Aedes (Stegomyia)* species relative to one another was calculated from the aggregate number of larvae in the monthly collections, expressed in percentage of the total (Table II). Seasonal changes in prevalence were determined from the percentages of cups that were positive for larvae of each species (Fig. 2). The two criteria were found to have a very close correlation; when the two sets of frequency distribution were compared for 9 *Aedes* species, the rank correlation coefficient r_s *was 0.998 (n being 13), indicating a very high statistical significance.*

As with the crepuscular collections of adults, a greater variety of species was encountered in the three sylvan environments than at the urban site among the larvae in the bamboo cups, although the number of species was lower than that coming to human bait.

In the forest relict (Table II, line b/t) Ae. apicoargenteus and *Ae. dendrophilus* accounted for 85 % of the larval prevalence between them, and at the two rural village sites *Ae. apicoargenteus* alone comprised 71-74 % of the larvae found in the bamboo cups. *Ae. aegypti* comprised 10 % of the larvae in the forest relict, 13-

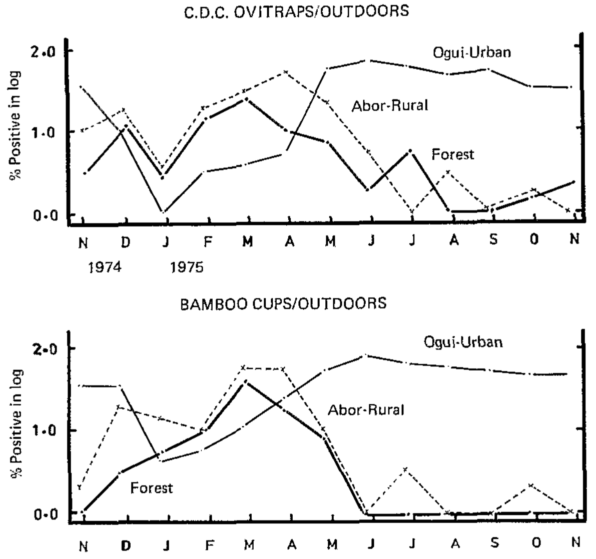

FIG. 2. – Seasonal changes in percentages of ovitraps and bamboo cups positive for *Aedes aegypti* larvae.

19 % in the rural villages, and 52 % at the urban site where the two preceding species were absent. At these 4 sites, the prevalences of *Ae. luteocephalus* were respectively 1 %, 4-6 % and 44 %. The numbers of *Ae. africanus* larvae found in the bamboo cups were low, and were zero in the urban biotope. *Ae. simpsoni* was found in small numbers at all the sites.

Larval prevalence in ovitraps : The numbers of *Stegomyia* species found in the CDC ovitraps attached to trees (Table II, c/t) were much less than in bamboo cups (b/t), but higher than those from ovitraps placed in compounds (c/c). The total number of larvae taken from the ovitraps placed in compounds were 30 % to 50 % less than the total collected from those attached to trees, due mainly to the large number of *Ae. apicoargenteus* in the wooded sites. At the urban site *Ae. aegypti*, predominated in ovitraps, its prevalence ranging from 81 % on tree-trunks to 95 % under caves in compounds; it was also the most prevalent species in the ovitraps exposed in the compounds in the two rural village sites. *Ae. luteocephalus* was second most prevalent species at the urban site; while in the rural villages where *Ae. apicoargenteus* predominated, it was more active in the compounds (2-4 % of the larval yields) than in the trees (1 % of the total larval yields). *Ae. africanus* was collected in ovitraps only from the relict, where more larvae were obtained from traps exposed at ground level than at a height of 1.5 m on tree-trunks (Table II).

Repeated soaking of ovitrap paddles : In order to ascertain how much additional hatching of larvae would be obtained by soaking the paddles 9 times instead of the 3 times employed throughout the study, 451 egg-positive paddles collected in November 1974 at the end of the rainy season, and 502 collected in April 1975 at the beginning of the next rainy season, were soaked 9 times at weekly intervals. The hatches obtained at each soaking (Table III) show that a 100 % hatch had been obtained after 3 soakings from the eggs collected in April at the beginning of the rainy season, but the eggs collected in November at the end of the rainy season showed a considerable additional hatch extending from the 4th to the 9th soakings. Assuming that the hatch had been completed after the 9th soaking (a questionable assumption) it can be seen that for late-season collections the 3-soaking routine employed in the field study had obtained only 8 % of the possible hatch for *Ae. simpsoni*, 53 % for *Ae. luteocephalus*, 60 % for *Ae. africanus* and 94 % for *Ae. aegypti*. For collections made at this season, it could be concluded from the results that to obtain a 95 % harvest of hatched larvae, the paddles would have to be soaked 9 times for *Ae. simpsoni* and *Ae. dendrophilus*, 8 times for *Ae. luteocephalus*, and 7 times for *Ae. africanus* and *Ae. apicoargenteus*.

The effect of this delay in the hatch of the late-rainy season eggs upon the results for the 6 *Stegomyia* species in November 1974 is evaluated in the calculations at the bottom of Table III. They show that in terms of absolute numbers *Ae. simpsoni* had been underestimated by more than 10 times and *Ae. aegypti* scarcely at all, while with the other species the figure had been about one-half of what it should have been. In terms of relative prevalence, however, the only gross errors had been the underestimation of the proportion of *Ae. simpsoni* and the overestimation of that of *Ae. aegypti*. It should be noted that the 3-soaking routine involved no such errors for the early rainy season eggs.

Seasonal cycle of larval prevalence : Results are presented in graphs for *Ae. aegypti* only, based on the percentages of positive ovitraps and bamboo cups in the urban and sylvan sites (Fig. 2). Following the dry season, an increase in frequency of larval infestation began first in the two sylvan environments in February as compared to May. Thereafter the larval infestations declined as the rainy season advanced, the decline being more marked in bamboo cups than in ovitraps and especially pronounced in the ovitraps attached to tree. In the urban environment (Ogui), larvae of *Ae. aegypti* did not begin to increase until May, and infestations were generally higher in bamboo cups than in ovitraps. *Ae. luteocephalus* also continued to breed in Ogui in bamboo cups throughout the dry season. Larval infestations of *Ae. simpsoni* in bamboo cups were confined to the dry months at all

TABLE III

Numbers of larvae obtained (percent hatch in brackets) from *Stegomyia* eggs in 9 different soakings of CDC ovitrap paddles collected at the beginning (April 1975) and end (November 1974) of the rainy season.

Soaking	*Ae. aegypti* Nov. '74	*Ae. aegypti* April '75	*Ae. luteocephalus* Nov. '74	*Ae. luteocephalus* April '75	*Ae. africanus* Nov. '74
1st	1 480 (67.6)	3 396 (89.6)	210 (12.2)	36 (40.0)	1 (0.7)
2nd	312 (14.4)	338 (8.9)	283 (17.3)	46 (51.1)	6 (3.9)
3rd	251 (11.8)	57 (1.5)	391 (23.7)	8 (8.9)	84 (55.3)
4th	55 (2.5)	0	289 (17.5)	0	38 (25.0)
5th	31 (1.4)	0	186 (11.4)	0	12 (7.9)
6th	9 (0.4)	0	55 (3.3)	0	2 (1.3)
7th	9 (0.4)	0	75 (4.5)	0	6 (3.9)
8th	17 (0.8)	0	73 (4.4)	0	1 (0.7)
9th	15 (0.7)	0	94 (5.7)	0	2 (1.3)
Total	2 189 (100)	3 791 (100)	1 656 (100)	90 (100)	152 (100)

Soaking	*Ae. simpsoni* Nov. '74	*Ae. simpsoni* April '75	*Ae. apicoargenteus* Nov. '74	*Ae. apicoargenteus* April '75	*Ae. dendrophilus* Nov. '74	*Ae. dendrophilus* April '75
1st	25 (1.7)	275 (87.6)	147 (5.3)	2 532 (62.9)	4 (3.3)	6 (46.2)
2nd	52 (3.5)	21 (6.7)	885 (31.9)	1 339 (33.2)	32 (6.5)	5 (38.5)
3rd	43 (2.9)	18 (5.7)	647 (23.3)	157 (3.9)	21 (17.4)	2 (15.3)
4th	209 (14.3)	0	594 (21.4)	0	29 (24.0)	0
5th	330 (22.3)	0	196 (7.1)	0	9 (7.4)	0
6th	133 (9.0)	0	86 (3.1)	0	3 (2.5)	0
7th	158 (10.8)	0	61 (2.2)	0	6 (4.9)	0
8th	418 (28.3)	0	97 (3.5)	0	5 (4.1)	0
9th	105 (7.1)	0	61 (2.2)	0	12 (10.0)	0
Total	1 473 (100)	314 (100)	2 774 (100)	4 022 (100)	121 (100)	13 (100)

Relative prevalence : November 1974, end of wet season.

		aegypti	*luteo-cephalus*	*africanus*	*simpsoni*	*apico-argenteus*	*dendro-philus*	*Total*
Based on 3 soakings	Number	2 043	884	91	120	1 679	57	4 874
	Percent	41.8	18.2	1.9	2.5	34.4	1.2	100
Based on 9 soakings	Number	2 189	1 656	152	1 473	2 774	121	8 365
	Percent	26.2	19.8	1.8	17.6	33.2	1.4	100

study sites, while larvae of *Ae. apicoargenteus* and *Ae. dendrophilus* in the forest relict became more abundant as the rainy season progressed. The monthly changes in larval prevalence determined by ovitraps are highly correlated with that in bamboo cups (Table IV).

Seasonal cycle of adult prevalence : Results are presented in graphs for *Ae. luteocephalus* in two inhabited sites (urban and rural), for *Ae. africanus* in two sylvatic environments (rural and forest) and for *Ae. aegypti* in all three study environments (Fig. 3); of the rural sites, Egede is not shown since its seasonal cycle was so similar to Abor. In both villages, the total catch of these three species exceeded 800 per 100 man-evenings, equivalent to 2 per man-hour, for the period of 10 months from March to December. The seasonal changes in the prevalence of *Ae. aegypti* followed closely the larval prevalences already observed and depicted as determined with ovitraps and bamboo cups (Table IV). It may be seen that the dry-season disappearance of mosquitoes, which usually begins in December or January, lasted much longer in urban Ogui than in the sylvatic environments. *Ae. aegypti* populations began to increase in February at Abor and its forest relict, followed by Egede in April and Ogui in May. In the two rural villages, the seasonal peak of this species occurred suddenly at the beginning of the rainy season and then gradually declined thereafter, while in Ogui the

TABLE IV

Correlation coefficients *(r)* for seasonal changes of *Aedes aegypti* adults and larvae as determined with different sampling methods in three study areas.

Sampling methods (1)	Study area		
	Ogui	Abor	Forest relict
Adult vs ovitrap/ compound (O/C)	0.615	0.724	0.886
Adult vs ovitrap/ trees (O/T)	0.563	0.986	0.677
Adult vs bamboo cup/ trees (B/T)	0.714	0.533	0.976
O/C vs O/T	0.923	0.618	0.767
O/C vs B/T	0.869	0.422	0.888
O/T vs B/T	0.942	0.869	0.765

(1) Adult-crepuscular landing-biting catches; The *r* values higher than 0.641 and 0.514 are statistically significant at the 1 % and 5 % levels, respectively.

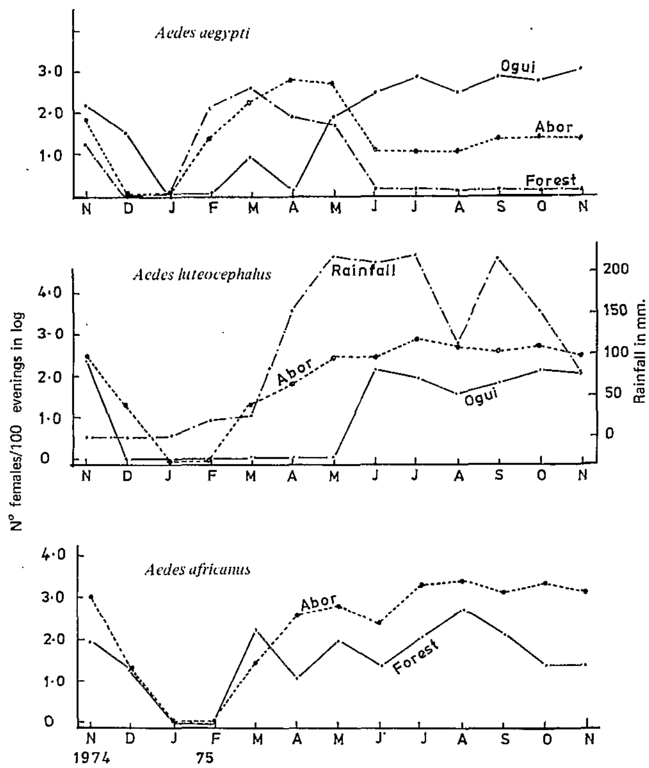

FIG. 3. – Relative abundance of the three most common vector species of *Aedes (Stegomyia)* caught during crepuscular hours on human baits in four biotopes in and near Enugu, Nigeria.

density progressively increased as the wet season advanced and the cover afforded by trees and shrubs became considerable. In the wooded environments, *Ae. luteocephalus* and *Ae. africanus* began to increase in March one month later than *Ae. aegypti*. In Ogui, however, *Ae. luteocephalus* did not appear in catches until June. Along with *Ae. africanus* in the wooded sites adult *Ae. luteocephalus* became slightly more prevalent in the second half of the rainy season, than in the first half, despite the reduction in larval prevalence that was observed during that later period in the rural areas.

DISCUSSION AND CONCLUSIONS

Among the known vectors of yellow fever, *Ae. africanus* appeared to be the most important species not only because of its high density in rural environment but also since it has recently yielded isolations of yellow fever among other arboviruses in derived and sub-sudanese savanna forests in West Africa (Chippaux *et al.*, 1975; Germain *et al.*, 1976).

In the vicinity of rural communities in the Udi Hills, the number of *Ae. africanus* caught at ground level was over two-thirds of the total *Aedes* species caught. Its biting rate exceeded the level of two females per man-hour during the first hour after sunset, ranging from 2.5 to 20.0 with an average of 8.7. The percentage taken in four crepuscular hours was about 90 %, which agreed with that found in the Lagos area of Nigeria (Mattingly, 1949) and the southern part of Cameroon (Rickenbach *et al.*, 1972). This species is known to bite throughout the night at canopy levels (Mattingly, 1949), from which more captures were made than at ground level (Haddow *et al.*, 1947; Rickenbach *et al.*, 1972). By contrast, in the mountainous northern part of the West Cameroon this species bite predominantly at ground level and during the day, which appears to be exceptional (Germain *et al.*, 1972). Its preference for higher levels remains to be studied in rural communities in derived savanna vegetation zones in eastern Nigeria.

Ae. luteocephalus is a widely distributed species in forest galleries in the sudanese savanna of West Africa (Hamon *et al.*, 1971), being considered an important vector of yellow fever following an epidemic on the Jos Plateau in 1969 (Lee & Moore, 1972). In rural communities in the Udi Hills, the numbers of this species caught on human baits were as much as those of *Ae. aegypti* (Table II), while in the urban areas and in the uninhabited forest relict they were about one-quarter as frequent as *Ae. aegypti*. It would be interesting to know whether *Ae. africanus* will be replaced by *Ae. luteocephalus* as forests are cut and rural communities become more urbanized. In the vicinity of Lagos *Ae. luteocephalus* outnumbered *Ae. africanus* in tree holes (Dunn, 1927), the latter being totally absent in urban Enugu (Table I). In eastern Senegal along the Gambia river, *Ae. luteocephalus* attacked man on a canopy platform more frequently than at ground level (Cornet, personal communication). Unlike its habit in western Senegal (Cornet & Chateau, 1974) no nocturnal activity was shown in the rural biotope in the Udi Hills in the Enugu area, although the biting rate within the first hour after sunset was found to range in this species from 2.0 to 5.5 per man-hour for seven of the rainy months. A biting rate in excess of 2 per man-hour is considered significant for the risk of arbovirus transmission (World Health Organization, 1972; Service, 1974).

As demonstrated in ovitrap surveys, the incidence of *Ae. aegypti* in ovitraps placed in compounds was always higher than that in open woods (Table II). However, during the months of heavy rain this species was more exophilic in its oviposition in the urban area, where it exceeded the other species in all the sampling methods employed. The biting cycle was characterized by prolonged activity in the afternoon, with a broad peak before sunset. This biting activity was unlike that which occurred in village huts on the Kenya coast surrounded by coconut plantations (McClelland, 1960) or in urban populations of Dar-es-Salaam (Trpis *et al.*, 1973), but was similar to that found in southeastern Nigeria among bushes between the village and surrounding rain forest (Boorman, 1960).

Ae. simpsoni was the fourth most common species among the *Stegomyia* species caught on human bait in the three human communities (Table I). The number caught biting was low, especially in view of the vast number of breeding habitats that are available during the rainy season (Bown & Bang, 1979). *Ae. sympsoni* has been reported as anthropophilic and diurnal at ground level in banana plantations near Yaoundé, Cameroon (Rickenbach *et al.* 1971), as originally observed in certain parts of Uganda (Gillett, 1951). By contrast, it appeared that most of the populations of *Ae. simpsoni* are strictly zoophilic (Hamon *et al.*, 1971). Nevertheless, in the Enugu region this species attacks man also, although not exclusively (Bow & Bang, 1979). *Ae. vittatus*, a suspected vector of yellow fever and one of the commonest *Stegomyia* species in northern Nigeria (Service, 1974), was recorded just once in the urban area during August. This species is unlikely to occur in large numbers as there are no rocky outcrops suitable for its breeding in the vicinity of the Udi Hills.

The seasonal fluctuations of the three most common vectors were positively correlated with the seasonal rainfall (Fig. 2), although they varied according to the species and the biotope. In wooded communities, *Ae. aegypti* increased abruptly following a few showers in February, but this species declined gradually as the rainy season advanced (Fig. 2 and 3) whereas females of *Ae. africanus* and *Ae. luteocephalus* increased (Fig. 3). This unusual seasonal decline in wooded communities can probably explain why *Ae. aegypti* was scarce in the 1969-1970 rural epidemics of yellow fever in Nigeria (Lee & Moore, 1972; Monath, 1972). When adult captures of these three species were combined, there were 10 months in which the crepuscular biting rate was higher than two females per man-hour with a range between 2.2 and 30.8. This rate would undoubtedly be supplemented when and where populations of *Ae. simpsoni* are anthropophilic, as in some other parts of Africa (Haddow *et al.*, 1947; Gillett, 1951; Rickenbach *et al.*, 1972).

From the present studies, it is concluded that the proper time for controlling adults by ultra-low-volume sprays is at twilight, since nearly 80 % of the biting activities of the four known vectors occurred during the crepuscular hours. On the other hand, larvicidal measures in domestic receptacles would not be effective, because greater numbers of these vectors breed in other habitats.

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